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RESPIRATION AND THERMAL TOLERANCE OF THE DUNGENESS CRAB, *CANCER MAGISTER* DANA

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Abstract—1. Routine and hyper-routine respiration and upper thermal tolerance were determined for *Cancer magister* in relation to acclimation temperatures 7.5 and 17.5°C.

2. Crabs acclimated to 17.5°C showed temperature insensitivity between 7.5 to 17.5°C for routine respiration.

3. Crabs acclimated to 7.5°C showed thermal sensitivity for all temperatures tested and an inverse acclimation pattern.

4. Hyper-routine rates showed thermal insensitivity from 7.5 to 17.5°C for both acclimation conditions and conformity from 17.5 to 22.5°C.

5. Thermal tolerance tests showed 17.5°C acclimated crabs resisted higher temperatures (33.5°C) than 7.5°C acclimated crabs (32.0°C).

6. No relationship was shown between death temperature and crab size.

INTRODUCTION

Projected development of saltwater cooled thermal electric plants increases the risk of thermal pollution in areas inhabited by commercially important species. Thermal adaptations of temperate zones marine invertebrates have been extensively studied, and it has become clear that most species are capable of some type of compensatory response (Vernberg & Vernberg, 1972). Compensatory modifications of metabolic rate fall into two major categories: (1) immediate responses in which metabolism is relatively insensitive to temperature change over some thermal range and (2) seasonal or acclimation responses which usually require some restructuring at the enzyme level and therefore a longer time for completion (Hochachka & Somero, 1973). Although these responses are prevalent among the marine invertebrates, the relative importance of the two categories and the overall magnitude of the compensatory abilities are species dependent variables. Little information of this type is available for commercially important species. In view of the increasing trend for thermal additions to marine waters, this lack of information seems particularly critical. In this study information is presented on the thermal adaptations of the Dungeness crab, *Cancer magister*, which has a wide geographical distribution along the western coast of North America—ranging from the Aleutian Islands, Alaska, to Magdalena Bay, Mexico. This crab is abundant in shallow water on sandy bottoms and ranges in depth from the low water line to about 100 fathoms (Butler, 1957). In the Puget Sound region of Washington, the adult crabs experience water temperatures ranging from 2.4 to 18.4°C (Cleaver, 1949).

Our objectives were to determine whether: (1) the metabolism of *C. Magister* would adjust in an adaptive manner when it was faced with elevated temperatures and (2) the upper lethal temperature limit would be altered with a change in acclimation temperature.

METHODS AND MATERIALS

Experimental animals

Collection—Adult male *C. magister*, collected in July 1970, were obtained from approximately 15 m of water in Chuckanut Bay near Bellingham, Washington. Water temperature and salinity during collection were 10°C and 29.9‰, respectively. All crabs were in an intermolt condition as determined by carapace hardness, coloration and cleanliness. Carapace widths (exclusive of lateral teeth) ranged from 13.5 to 19.1 cm and whole weights from 343.6 to 1070.3 g. The carapace of each crab was marked using a vibrating pencil for individual identification. No animal was used more than once in a respiration test. Respiration data were obtained on 64 crabs and upper temperature tolerance was obtained for all but 2 of the same crabs.

Acclimation—Test animals were maintained in 29‰ seawater under static conditions at one of two acclimation temperatures, 7.5 or 17.5°C (±0.5), for 13–15 days prior to a respiration test. Two additional days of acclimation followed each respiration test before determining the upper thermal limit. The crabs were maintained under continuous artificial illumination and were not fed during the acclimation period. Water was changed at least once a week and fecal material removed daily.

Respiration experiment

Respiration tests were conducted in a recirculating flow-through respirometer. The system consisted of five respirometer chambers—four test and one control. Each respirometer chamber had a fiberglass housing, two removable end plates, and fittings (Fig. 1).

* The work reported here was part of a Thesis submitted by the senior author to the Graduate School, Western Washington University, in the partial fulfillment of the requirements for the Master of Science Degree.

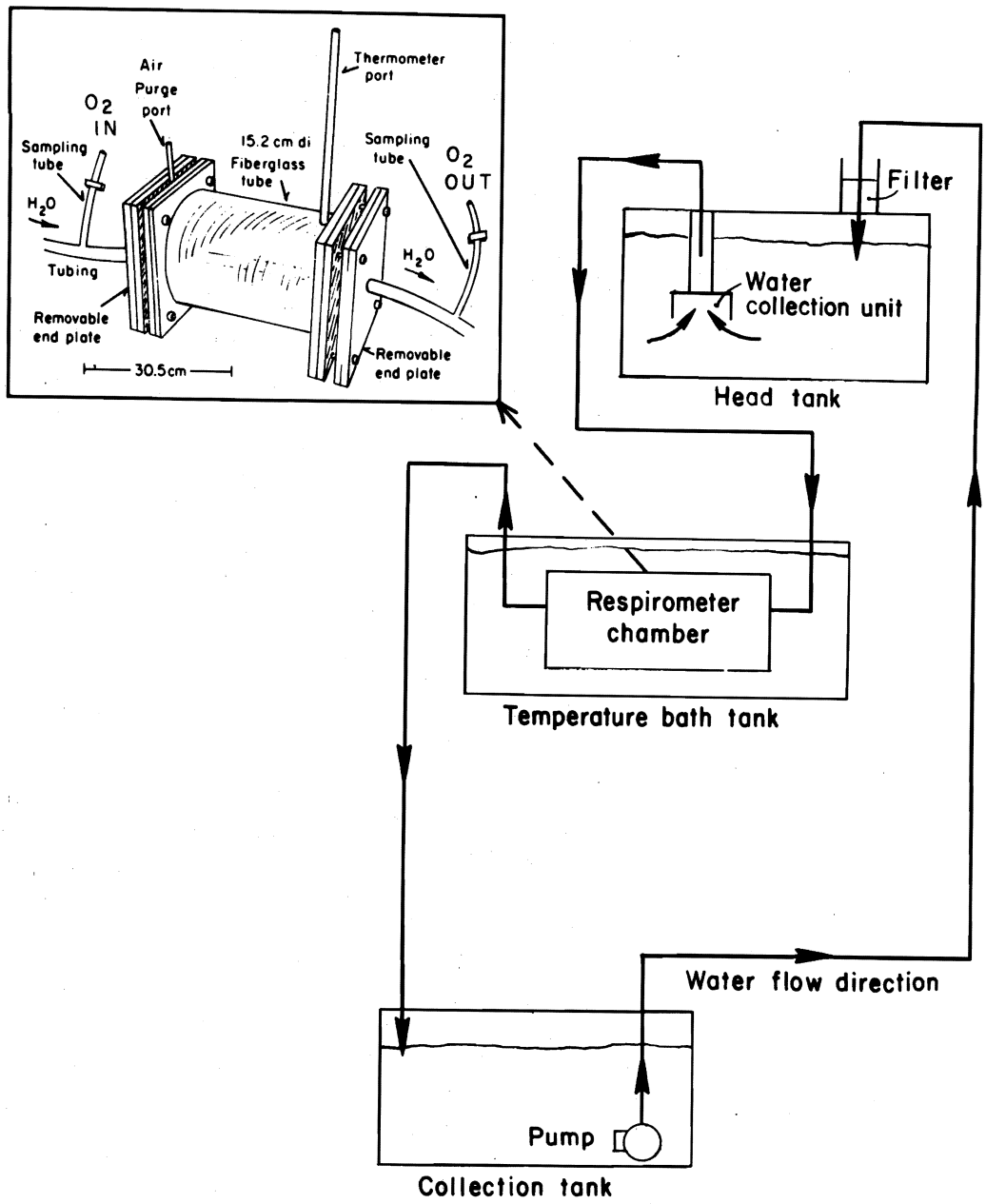

Fig. 1

A head tank maintained a constant hydrostatic head (±0.04 cm) which supplied the five respirometers with a constant temperature water bath. A battery of air stones within the head tank insured complete water aeration and circulation. Water was drawn from a common area within the head tank and gravity fed through equal length tubes (Tygon* was used exclusively in the system) to the respirometers. A submersible pump insured uniform water circulation and temperature within the water bath housing the respirometers. Discharge from the respirometers entered a common collection tank where it was aerated and pumped to an oyster shell-charcoal filter located on top of the head tank. The water flow from each respirometer was controlled with a screw pinch clamp. At the end of five 9-hr test periods, all water within the system was replaced with fresh seawater. The filter material was replaced at the same time. All tests were conducted under continuous artificial illumination.

Five respiration runs were made at each test temperature: 7.5, 17.5, and 22.5°C, and a single test was conducted at 27.5°C. In each run, two crabs from each of the two acclimation temperatures were placed in individual respirometer chambers. A fifth chamber was used as a control blank.

All tests were conducted for a period of 9 hr. At the termination of each test, the animals were returned to their respective acclimation aquaria.

Oxygen consumption was calculated using the following expression:

$$\mu l\ O_2/ghr = (O_2)_i - (O_2)_0 \times F \times 1/W$$

where $(O_2)_i$ is the concentration of oxygen entering a respirometer chamber and $(O_2)_0$ is the concentration of

* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1. Mean water test temperature and flow rate in respirometer chambers for warm and cold acclimated Dungeness crabs at test temperatures of 7.5, 17.5, 22.5 and 27.5°C

Test temperature (°C)	Cold acclimated (7.5°C)				Warm acclimated (17.5°C)			
	Flow liter 1/hr		Temp. (°C)		Flow liter 1/hr		Temp. (°C)	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
7.5	15.4	3.62	7.5	0.20	16.3	2.89	7.5	0.20
17.5	15.2	2.35	17.5	0.11	15.7	1.66	17.5	0.11
22.5	18.1	1.49	22.5	0.13	15.6	1.75	22.5	0.13
27.5	15.9	6.75	27.6	0.09	12.6	7.47	27.6	0.09

oxygen leaving. F is the water flow rate through a chamber in liters per hour and W is the wet weight of the whole animal.

Water samples from the inflow and outflow of each respirometer chamber were taken hourly during each test run except for those at 27.5°C, where they were taken at 30 min intervals. Water flow rate and temperature were determined for each chamber after sampling (Table 1). Oxygen content of the samples was determined by the Winkler method as described by Strickland & Parsons (1968).

Thermal tolerance experiment

Thermal limit tests were conducted on crabs which had previously undergone respiration tests and reacclimation, with the exception of two crabs which were taken directly from the field.

A 230 liter insulated tank was used as a testing container. Water was continuously aerated, filtered, and circulated within the container. Three 500 W rheostat controlled submersible heaters were used in heating the water.

The tests were conducted at a constant heating rate of 0.5°C per min starting from a base temperature of 7.0°C. This procedure has, in part, been followed by Tsukada & Ohsawa (1958), Tsukada (1961), and Hutchison (1961). The water temperature was recorded every 10 min with more numerous readings being recorded as lethal temperatures were approached. The criterion for death was the lack of scaphognathite movement upon probing a crab. After the apparent death of each crab, the water temperature was recorded and the crab returned to its acclimation tank for 30 min of post-test observation. The filter and water in the test tank were changed after each test.

RESULTS AND DISCUSSION

Respiration

The respiration data obtained were subjected to Duncan's multiple range test (Steel & Torrie 1960) to determine significance at the 95% confidence level. Multiple regression analysis was used to determine the variability of respiration rate in relation to acclimation temperature, test temperature, and body weight.

Ten warm (17.5°C) and 10 cold (7.5°C) acclimated crabs were tested at each temperature (7.5, 17.5, and 22.5°C). A minimum of nine oxygen readings, one per hr, were taken on each crab tested. The mean of the three lowest readings for each crab was chosen to exemplify routine respiration.

The higher readings were eliminated as they presumably represented oxygen consumption at an elevated activity level. The mean oxygen consumption of the cold or warm acclimated crabs at each test temperature was averaged and plotted (Fig. 2). The resulting pattern using the three lowest readings was the same as when the mean of all nine readings was used, except that absolute values varied. Oxygen consumption was significantly higher for the warm compared to the cold acclimated crabs tested at 7.5°C. No differences in rate of oxygen consumption were shown for test temperatures of 17.5 and 22.5°C between acclimation groups. Using Precht's (1958) classification scheme, cold conditioned crabs showed an inverse acclimation pattern (Type 5) and warm conditioned crabs showed no acclimation (Type 4). Cold acclimated crabs showed a significant ($P < 0.05$) rate difference between test temperatures of 7.5 to 17.5°C ($Q_{10} = 2.23$) and 17.5 to 22.5°C ($Q_{10} = 3.57$), indicating conformity to temperature for routine respiration. The Q_{10} value represents the change in metabolic rate in response to a 10°C temperature change as in the van'T Hoff equation (Giese, 1963). The warm acclimated group showed no significant rate difference between test temperatures of 7.5 to 17.5°C ($Q_{10} = 0.93$), but a significant ($P < 0.05$) difference was observed between 17.5 to 22.5°C ($Q_{10} = 4.51$). Routine respiration of warm acclimated *C magister* is therefore insensitive to acute temperature change over a wide thermal range. The overall Q_{10} (7.5 to 22.5°C) for cold and warm acclimated crabs was 2.62 and 1.58, respectively.

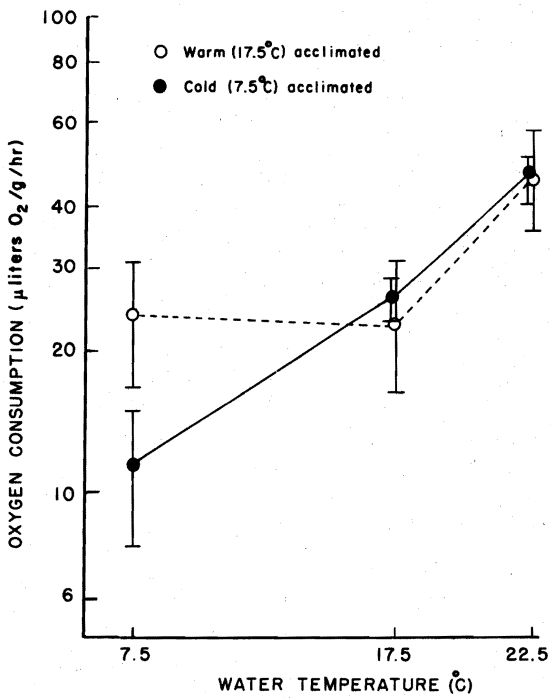

Fig. 2

The routine metabolic rates were subjected to a multiple regression analysis in which the variables of interest were designated acclimation temperature, test temperature, and crab body weight. Test temperature accounted for 50% of the variability while weight and acclimation temperature accounted for 3% and 0.4%, respectively. The prediction formula, based upon a straight line relationship, is:

$$\text{Resp. rate} = 9.550 + 1.824\,(\text{test temp.}) - 0.015\,(\text{body wt.})$$

Based on the above formula, respiration rate can be predicted within a standard error of 11.7 μl O_2. It is not beneficial to know the acclimation temperature. The predicted rate of metabolism at 10°C is in reasonable agreement with the measurements made at that temperature by Johansen *et al.* (1970) using closed system respirometry.

Preliminary experiments (based on notes of the senior author) on respiration of isolated tissues from cold (7.2°C) and warm (18.8°C) acclimated *C. magister* indicated that the pattern of thermal acclimation of nerve tissue is similar to that seen for routine metabolism in the whole animal. Isolated ventral nerve cords from warm acclimated crabs had significantly ($P < 0.05$, $n = 4$) higher rates of respiration than similar tissue from cold acclimated crabs at all test temperatures over the range 0.5 to 30.0°C, indicating an inverse (Precht Type 5) acclimatory response. Gill and heart tissue showed partial compensatory shifts (Precht Type 3) with thermal acclimation at most test temperatures while muscle tissue showed no compensatory response (Precht Type 4). The results of these preliminary experiments are consistent with the view that the central nervous system is important in determining the metabolic response of the whole animal during thermal acclimation (Prosser *et al.*, 1965). Unfortunately, similar experiments with other crustaceans have failed to uncover a consistent relationship between the metabolism of isolated tissues and the whole animal (Roberts, 1957b; Vernberg & Vernberg, 1966a).

Inverse acclimatory responses are not commonly encountered when dealing with whole animal metabolism and their adaptive significance is frequently obscure. Hazel and Prosser (1970) considered two explanations that could be pertinent at the whole organism level: (1) the organism may not remain behaviorally active at low temperatures, thus negating any benefits from metabolic compensations and (2) secondary factors such as oxygen availability, nutritional state, or salinity may interact in such a way as to obscure or override compensatory responses to temperature. Examples of this second explanation are Krog's (1954) study of amphipod metabolism, where low oxygen during periods of ice cover influenced the adaptive response, and Dehnel's (1960) study of respiration of shore crabs of the genus *Hemigraphsus*, where both salinity and temperature were varied simultaneously. In the study of Hulbert *et al.* (1976) with *H. nudus*, when salinity was removed as a variable, a moderate tendency for partial compensation (Precht Type 3) was observed. In the present study the only secondary variable that seems likely to interact with the effects of temperature is the nutritional state of the crabs. To reduce variation from differences in food acceptance, to insure a post absorptive state during metabolism measurements, and for convenience of care in the static holding facilities, the crabs were not fed during the acclimation period.

The effects of starvation on the metabolic rate of crustaceans appear to be quite variable. In some cases metabolism declines over a several-day period and then stabilizes at a new lower level (Roberts, 1957a; Vernberg, 1959a). Other workers have shown little or no decrease in respiration rate with starvation (Thomas, 1954; Barnes *et al.*, 1963). The procedure of starvation, although insuring the animal is in a post-absorptive state, may interfere with its acclimation process. Vernberg (1959b) found the crab *Uca* would continue to acclimate for up to 21 days if fed, but that after 6–8 days of starvation the crabs lost their acclimation ability. No investigation was performed on *C. magister* to determine the effect of starvation upon metabolic rate or acclimation. Although starvation may have influenced the results of this study, the fact that there was a significant acclimation effect suggests that some active adjustment of metabolism was still possible. The animals with the lowest metabolic rate were the cold acclimated crabs run at 7.5°C. These experimental conditions are least likely to be stressful from the standpoint of depletion of endogenous nutrient stores.

The mean rate of oxygen consumption for warm and cold conditioned crabs at each test temperature for the three highest readings (hyper-routine respiration rate) is shown in Fig. 3. The respiration pattern shown was constant for the single highest as well as the mean of the six highest readings analyzed; only the absolute rate changed. No significant differences (0.5 probability level) were found between the two acclimation groups at all test temperatures, indicating no acclimatory response (Precht Type 4) for hyper-

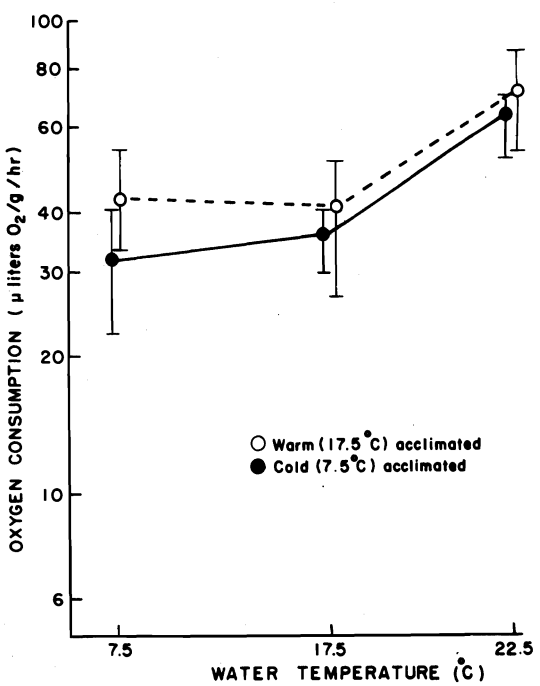

Fig. 3

routine metabolism. In both acclimation groups no significant respiration differences (0.05 probability level) were found between test temperatures 7.5 to 17.5°C (cold acclimated $Q_{10} = 1.08$, warm acclimated $Q_{10} = 0.92$), indicating thermal insensitivity of hyper-routine metabolism over this temperature range. Respiration rates were significantly different ($P < 0.05$) in both acclimation groups between test temperatures of 17.5 to 22.5°C (Cold acclimated $Q_{10} = 3.40$, warm acclimated $Q_{10} = 2.96$), indicating a thermal conformity of hyper-routine metabolism over this higher temperature range. The overall Q_{10} (7.5–22.5°C) for cold and warm acclimated crabs was 1.59 and 1.36, respectively. Newell (1969) suggested that temperature affects the active rate of oxygen consumption much more than the standard rate. This differs with the results of the present study, which showed the routine (standard) rate with a higher overall Q_{10} for both acclimation groups (2.62 cold; 1.58 warm) than the hyper-routine active rate with overall Q_{10}'s of 1.59 (cold) and 1.36 (warm). The explanation for the discrepancy between the two studies is not obvious. The levels of activity in the two studies may have been different although a somewhat similar means of deriving the values was used.

The means of the highest three respiration values (hyper-routine) were subjected to regression analysis in reference to the aforementioned variables of interest. Test temperature accounted for 26.0% of the variability, while weight and acclimation temperature accounted for 8.5% and 2.5%, respectively. Based upon a straight line relationship the prediction formula is:

Resp. rate = 40.147 + 1.727 (test temp.) − 0.033 (body wt.) having a standard error of 16.7 μl O_2.

One of the most striking features of our results is the general lack of temperature sensitivity of metabolism within the normally expected range of environmental temperatures for *C. magister*. Only the cold acclimated crabs seem to show a depressed rate of routine metabolism at the lowest temperature. Stated in another way, the Q_{10} for routine metabolism is inversely related to acclimation temperature over the normal temperature range. A number of studies have indicated that a pattern of higher Q_{10} with low acclimation temperatures is not at all uncommon among crustaceans (Roberts, 1957b; Teal, 1959; Vernberg, 1959b; Vernberg & Vernberg, 1966b). Teal (1959) suggested that a high Q_{10} would be adaptive to low temperatures. The decrease in metabolic rate with decreasing temperatures reduces the activity level of the animal (thus, its ability to gather food), but at the same time it results in a conservation of food reserves.

The seasonal behavior pattern of *C. magister* suggests an explanation for the routine respiration pattern shown. This species shows a migration trend toward deep water in the winter and toward shoal waters during the summer. However, this pattern is not fixed since the crab can be found in all water depths year-round (Cleaver, 1949). Marine water temperatures are generally considered more stable at depth and during winter months as compared to the intertidal area and summer months (Collias *et al.*, 1966). Thus, the crab would encounter greater temperature extremes during the summer months than during winter. If cold acclimation represents winter and warm acclimation summer conditions, then the greatest thermal variation would be experienced by the warm acclimation group. Morris (1961) and Barlow (1961) have suggested that a low Q_{10} is adaptive for conditions of varying habitat temperatures. In the case of the warm acclimated crabs, a Q_{10} of 0.93 was shown for the temperature range of 7.5–17.5°C in comparison to a Q_{10} of 2.23 for cold acclimated crabs in the same temperature range. The normal summer habitat temperature for the crabs is within the temperature range in question.

Thermal stress may account for the high Q_{10} values in the temperature span of 17.5–22.5°C for both acclimation groups (warm acclimated $Q_{10} = 3.57$, cold acclimated $Q_{10} = 4.51$). This assumption is partially supported by the single respiration test conducted at 27.5°C on two warm and two cold acclimated crabs. The respiration pattern is shown in Fig. 4. At the end of the tenth reading (30-min periods), a total exposure time of 5.5 hr, both cold acclimated crabs were dead. The two warm acclimated crabs were inactive upon removal from the respirometers but seemed to recover completely after being placed back in 17.5°C water (acclimation temperature) for 12 hr. The two acclimated crabs appeared to have expired before the first reading (2.6 and 3.6 μl O_2/g/hr, respectively). The pattern shown for the cold acclimated crabs may

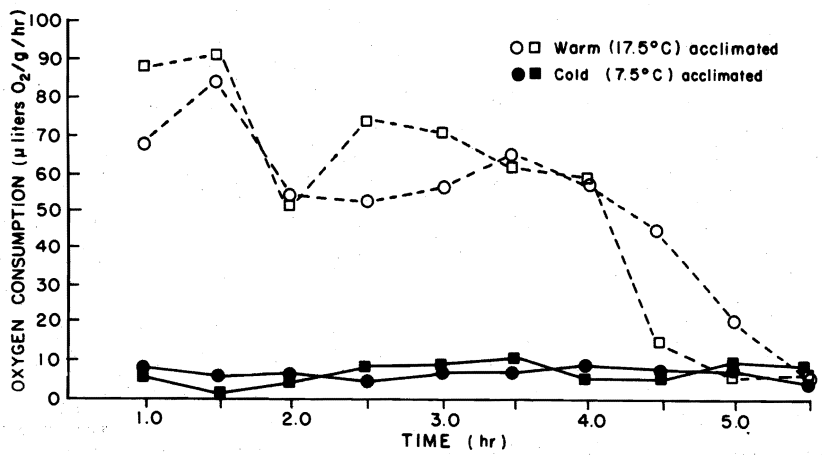

Fig. 4

be due to tissue respiration after death of the animal (Bowler, 1963) or to bacterial decomposition. The decrease in respiration rate shown by the warm acclimation group after 2 hr of exposure may be due to heat coma as discussed by Tsukuda (1961). It is interesting to note that Florey & Kriebel (1974) found a decrease in the heart rate of *C. magister* at a temperature of 25°C. Furthermore they report irreversible damage to the crabs at this high temperature.

The effect of temperature on the metabolic rate of *C. magister* may parallel the temperature effect on heart rate. Florey & Kriebel (1974) report a rather uniform increase in heart rate ($Q_{10} = 2.0$) over the temperature range of 4–19°C for crabs acclimated to 11°C for an unspecified length of time. The overall Q_{10} for our crabs acclimated to 7.5°C for the temperature range of 7.5–22.5°C was 2.62, a value not too dissimilar from theirs. The differences in acclimation temperature and the rather obvious departure from a linear response of metabolism at higher acclimation temperatures make the relationship between these two physiological parameters difficult to evaluate.

Thermal tolerance

A *t*-test for a difference between two independent means was used to compare the lethal temperature of crabs as a function of acclimation temperature. Weight and size of crabs were tested for correlation with death temperature using Pearson's product-moment correlation test (Steel & Torrie, 1960). The mean death temperature for cold acclimated crabs was 32.0°C; that of warm was 33.5°C. The difference is significant at the 0.001 level ($t = 4.495$, d.f. = 58). The death temperature of two crabs directly out of the field (11°C) was 32.9°C and 33.2°C. The acclimation pattern shown is compensatory with respect to the temperature change in contrast with the pattern shown for routine respiration. No significant difference (95% confidence interval) was found between the size (width or weight) of either warm or cold acclimated crabs and death temperature.

SUMMARY

Respiration rates were determined for the crab *Cancer magister* in relation to two acclimation temperatures (7.5 and 17.5°C). Respiration tests were conducted in a recirculating flow-through respirometer at 7.5, 17.5, 22.5, and 27.5°C. All crabs were starved during a 2-week acclimation period prior to testing.

Routine respiration of crabs acclimated to 17.5°C was insensitive to temperature change between 7.5–17.5°C, while crabs acclimated to 7.5°C showed thermal sensitivity for 7.5, 17.5 and 22.5°C. Crabs acclimated to 7.5°C showed an inverse acclimation pattern. The overall Q_{10} (7.5–22.5°C) for cold and warm acclimated crabs was 2.62 and 1.58, respectively.

The routine metabolic rates were subjected to multiple regresssion analysis in which acclimation temperature, test temperature, and body weight were the variables of interest. Test temperature accounted for 50% of the variability while weight and acclimation temperature accounted for 3% and 0.4%, respectively. The routine metabolic rate prediction formula, based upon a straight line relationship, was:

Resp. Rate Routine = 9.550 + 1.824 (test temp.) − 0.015 (body wt).

Based on the formula, respiration rate can be predicted within a standard error of 11.17 μl O_2. "Hyper-routine" respiration rates showed a pattern of thermal insensitivity at low temperatures (7.5–17.5°C) for both acclimation conditions and conformity at high temperatures (17.5–22.5°C).

"Hyper-routine" respiration was subjected to regression analysis in reference to the aforementioned variables of interest. Test temperature accounted for 26.0% of the variability, while weight and acclimation temperature accounted for 8.5% and 2.5%, respectively. Based upon a straight line relationship the prediction formula was:

Resp. rate (hyper-routine) = 40.147 + 1.727 (test temp.) − 0.033 (body wt) having standard error of 16.71 μl O_2.

The results showed the crab's metabolism to be generally temperature insensitive within its normal range of environmental temperature. Only cold acclimated crabs seemed to show a depressed rate of routine metabolism at the lowest temperature. The seasonal migration pattern of the crabs suggests the adaptive significance of the above.

Upper thermal tolerance tests were conducted in a water bath raised 0.5°C/min. These tests showed that warm acclimated crabs resisted higher temperatures (33.5°C) than cold acclimated crabs (32.0°C). No relationship was shown between death temperature and crab size.

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